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Distribution, abundance and population structure of Protura in two woodland soils in Southwestern Sweden

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With one figure

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1. Introduction

The Protura are mainly soil inhabitants with a wide global distribution. The humus layer seems to be their preferred microhabitat. STURM (1959) observed their feeding behaviour and found them sucking on hyphae and mycorrhiza. Few ecological investigations have been focused on Protura, perhaps partly because they seldom have been obtained in high numbers from soil samples. Although they may be less common than the most abundant microarthropods in soil, they are well suited to population studies.

Protura populations are usually composed of four larval stages (the males having five) in addition to adults (TUXEN 1961, 1964). The larval stages are: praelarva, larva I, larva II, maturus junior and praeimage (only the males). Larvae reach adult stage by anamorphosis, which permits age structure analysis.

The dispersion of animals could give valuable information about the relationships between the animal and its environment. The distribution of soil animals have been investigated e.g. by SALT et al. (1948), who suggested that soil arthropods usually were aggregated. Later studies support that conclusion (e.g. POOLE 1961 about Collembola, NEF 1962 about Acarina). The reasons for the aggregated distribution are not fully understood.

To be able to deal with population biology, and especially population dynamics, knowledge of the age structure of the investigated population is necessary. TUXEN (1949) made a comprehensive study on two Protura species in a Danish beech wood, but further information about population biology of Protura is scarce. Also the relationship between different species in natural habitats is poorly known. A list with some known Proturan synusies in Europe is given by NOSEK (1975).

The aim of this study is to compare Protura populations in an oak and spruce woodland area. Results regarding distribution, abundance, population structure and species composition are discussed.

2. Material and methods

2.1. Sampling sites

This study concerns two localities, an oak wood at Gunnebo and a spruce stand at Härkeshult, both east of Gothenburg, SW Sweden. In the oak wood, which was thinned some years ago, shrubs are presently growing rapidly. *Quercus* sp. dominates among the trees. The most frequent shrubs are *Rhamnus frangula* L. and *Quercus* sp. Also the herbaceous vegetation is well established with *Deschampsia flexuosa* (L.) as dominating and *Vaccinium myrtillus* L., *V. vitis-idaea* L. and *Pteridium aquilinum* (L.) as frequent plants. The humus layer is thick (about 10 cm) and a podzol is developing.

In the spruce stand, which also has been thinned, *Picea abies* (L.) is the only tree growing on the plot. Herbaceous vegetation is almost missing, except for a few tufts of *Deschampsia flexuosa*. There are also some *Dicranum* and other Bryophyta stands. A soil profile shows a well developed podzol with a felty, thick (about 10 cm) raw humus.

Table 1a. Environmental Factors: Soil water content and field capacity

Site and date	Habitat	n	Soil water content		Field capacity	
			Mean (vol%)	S.E.	Mean (vol%)	S.E.
Gunnebo 10 Oct. 1976	Oak	3	*25*	2.4	*51*	6.3
Härkeshult 11 Oct. 1976	Spruce	3	*23*	0.9	*53*	1.4

Table 1b. Environmental Factors: Acidity

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Site and date	Habitat	n	pH (dist. H_2O)		pH (0.2 M KCl)	
			Mean	S.E.	Mean	S.E.
Gunnebo 10 Oct. 1976	Oak	10	4.5	0.06	3.6	0.09
Härkeshult 11 Oct. 1976	Spruce	10	3.9	0.05	2.9	0.04

Table 2. Protura distribution

A. Oak wood at Gunnebo, 10 October 1976

Sample	G1	G2	G3*)	G4	G5*)	G6	G7	G8	G9	G10	Sum G1–G10
Numbers of Protura	28	5	–	37	–	16	3	21	1	3	114

B. Spruce stand at Härkeshult, 11 October 1976

Sample	H1	H2	H3	H4*)	H5	H6	H7	H8	H9	H10	Sum H1–H10
Numbers of Protura	6	62	0	–	36	177	1	12	1	12	307

C. Spruce stand at Härkeshult, 9 November 1976

Sample	H11	H12	H13	H14	H15	H16	H17	H18	H19	H20	
Numbers of Protura	50	61	4	8	17	38	34	70	3	15	
Sample	H21	H22	H23	H24	H25	H26	H27	H28	H29	H30	Sum H11–H30
Numbers of Protura	16	9	27	48	3	6	3	9	43	62	526

*) Sample inadvertently destroyed during extraction.

Table 3. Aggregation: Index of aggregation (λ) and χ^2-test for agreement with a Poisson series, on the dispersion index of Fisher

Site and date	Habitat	λ	χ^2 value	d.f.	χ^2 probability*) level
Gunnebo 10 Oct. 1976	Oak	3.34	77.95	7	$p < 0.001$
Härkeshult 11 Oct. 1976	Spruce	9.26	685.94	8	$p < 0.001$
Härkeshult 9 Nov. 1976	Spruce	4.29	349.95	19	$p < 0.001$

*) Probability of error.

Table 4. Estimation of Protura densities

Site and date	Habitat	n	Mean (numbers/soil core)	S.E.	Mean (numbers/m²)	S.E.
Gunnebo 10 Oct. 1976	Oak	8	14.3	4.46	3500	1100
Härkeshult 11 Oct. 1976	Spruce	9	34.1	18.0	8400	4400
Härkeshult 9 Nov. 1976	Spruce	20	26.3	4.92	6500	1200

Table 5. Population structure of Protura in oak wood at Gunnebo in 10 October 1976

Sample	*E. delicatum*			*E. germanicum*			*E.* sp.			Undetermined	Remaining larvae:		Total
	MJ	♀	♂	MJ	♀	♂	MJ	♀	♂		larva I	larva II	
G1	0	0	0	7	8	7	0	0	0	0	3	3	**28**
G2	0	0	0	1	3	0	0	0	0	0	0	1	**5**
G4	1	2	2	1	7	2	0	0	0	2	6	14	**37**
G6	1	0	0	0	5	1	0	0	0	2	1	5 (+1)*)	**15 (+1)**
G7	0	0	1	0	0	0	0	0	0	0	1	1	**3**
G8	0	3	1	1	7	3	1	1	0	2	1	1	**21**
G9	0	0	0	0	0	0	0	0	0	1	0	0	**1**
G10	0	0	1	0	0	0	0	0	0	0	0	2	**3**
Σ	**2**	**5**	**5**	**10**	**30**	**13**	**1**	**1**	**0**	**7**	**12**	**27**	**113 (+1)**

*) A larva of an Acerentomidae sp.

"MJ" = maturus junior, possible praeimagines are placed together with the males. "Undetermined" indicates MJ, ♀ and ♂ specimens not determined to species and/or damaged specimens.

Table 6. Population structure of Protura in spruce stand at Härkeshult in 11 October 1976

Sample	*E. delicatum*			*E. germanicum*			*E.* sp.			Undetermined	Remaining larvae:		Total
	MJ	♀	♂	MJ	♀	♂	MJ	♀	♂		larva I	larva II	
H1	0	1	0	1	0	2	1	0	0	1	0	0	**6**
H2	0	0	0	13	11	7	0	2	0	11	13	5	**62**
H5	0	0	0	8	5	4	0	0	3	12	4	0	**36**
H6	0	1	1	12	23	31	1	2	3	39	55	9	**177**
H7	0	0	1	0	0	0	0	0	0	0	0	0	**1**
H8	0	0	0	2	1	1	3	0	0	0	4	1	**12**
H9	0	0	0	0	1	0	0	0	0	0	0	0	**1**
H10	0	0	2	0	1	1	2	2	0	4	0	0	**12**
Σ	**0**	**2**	**4**	**36**	**42**	**46**	**7**	**6**	**6**	**67**	**76**	**15**	**307**

"MJ" = maturus junior, possible praeimagines are placed together with the males. "Undetermined" indicates MJ, ♀ and ♂ specimens not determined species and/or damaged specimens.

Three environmental factors were investigated. Soil down to a depth of 5 cm was taken at random for analysis of water content (three samples), field capacity (three samples) and acidity (ten samples). This was done at each site during the October samplings (see 2.2.). The soil water content and field capacity were determined by gravimetry. The acidity of the soil was measured with a pH-meter after extraction with distilled water or 0.2 M potassium chloride. The results are summarized in tables 1a and 1b. The soil of the spruce stand was 4—5 times more acid than the oak wood soil. The humidity situations seemed to be comparable in the two soils. In all cases the standard errors were greater in the samples from the oak wood, compared with the spruce soil samples. This may indicate a more heterogenous environment in the oak wood soil.

2.2. Sampling methods

Ten soil samples were taken at random at each of the two study areas (table 2). The cylinder of soil for a single sample had a surface area of 40 cm² and a depth of 5.0 cm. At sampling the litter layer was excluded. A first set of samples was brought from the oak wood at Gunnebo in 10 October 1976 and from the spruce stand at Härkeshult in 11 October 1976. At Härkeshult a second set, comprising twenty soil samples, was taken at random in 9 November.

2.3. Extraction technique and its efficiency

The Protura were extracted from the undisturbed and inverted soil samples by a dynamic method described by Kempson et al. (1963). This method is recommended by Edwards & Fletcher (1971) for Protura in woodland soils. The construction of the apparatus was simplified by using three 75W-bulbs, lighting in sequence, instead of an infrared lamp.

During extraction of the October samples the minimum temperature difference between the air above the soil cylinders and the water bath below them, was 11 °C. The maximum difference, at the end of the extraction period, was 36 °C. The November samples were extracted with a minimum difference of 16 °C and a maximum difference of 25 °C. Both extractions were carried out during a period of eight days.

No efficiency test has been made, but this method obviously only gives a certain proportion of the total population. The praelarvae are completely missing in the catch (see tables 5 and 6). It is probably not easy to obtain praelarvae using a dynamic method, since they may be in a resting stage (Tuxen 1964). However, samples given exactly the same treatment, as the soil cores from 10 and 11 October, should be possible to compare. The original apparatus was tested by Kempson et al. (1963) giving an efficiency between 75—100 % for Collembola.

2.4. Preservation and mounting

The specimens were first collected in approximate 50 % picric acid, then stored in 80 % ethanol before they were mounted in polyvinyl lactophenol.

3. Results

3.1. Protura distribution

The distribution patterns of Protura found in forty soil samples are summarized in table 2. The number of animals in a single soil core is varying between 0 to 177 specimens. In figure 1 the relative abundances of cores with reference to the number of animals in each core are shown for the three sets of sampling. Also the total of samples (n = 37) is shown as a comparison. In spite of the small number of cores taken, it seems as the agreement between the samplings is satisfying. The first class (0—9 specimens in a soil core) is 50 % (n = 8) in the oak wood, 44 % (n = 9) in the first and 40 % (n = 20) in the second spruce sampling, for the total of samples it is 43 % (n = 37).

Whether the dispersion is random, regular or clumped can be tested by a χ^2-test for agreement with a Poisson series, i.e. the random distribution type. The expected ratio between variance (s^2) and mean ($\bar{x}$) with random distribution = 1, whereas aggregation increases the ratio $s^2/\bar{x}$. The index of aggregation is defined as $\lambda = (s^2/\bar{x})^{1/2}$. Transforming λ into the dispersion index of Fisher, its significance can be tested (see Debauche 1962). This is done in table 3. In all three sets of sampling, the Protura distribution turned out to be aggregated.

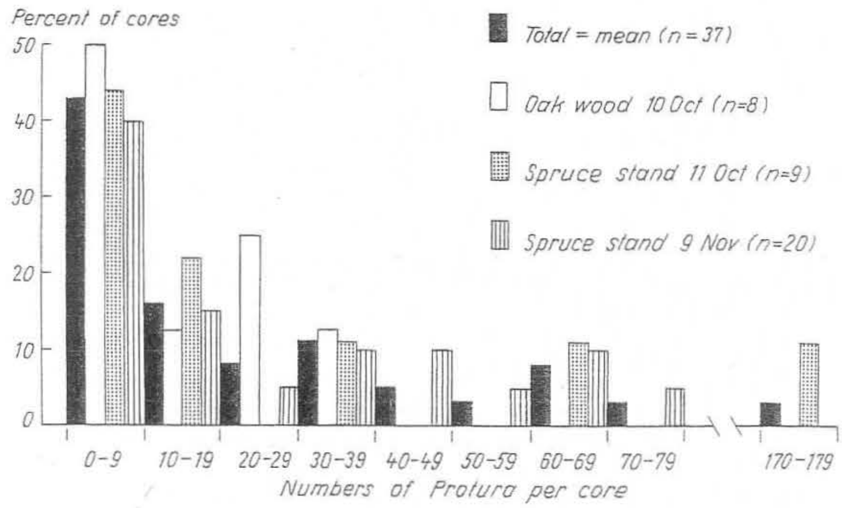

Fig. 1. Relative abundances of cores with reference to the number of Protura in each core. Data are given for the three sets of sampling and for the total of the samples.

3.2. Protura population densities

Estimates on population densities from the three sets of sampling are summarized in table 4. These estimates refer to the upper 5 cm of the soil profile. In the oak wood soil the mean was $3500/m^2$ (S.E. = 1100) and in the spruce stand soil $8400/m^2$ (S.E. = 4400) in October and $6500/m^2$ (S.E. = 1200) in November. In all cases the standard errors are high, partly due to the aggregation.

3.3. Protura population and species structures

A total of 947 specimens were collected during extraction of the three sampling sets 421 specimens, i.e. from the samples taken in the oak wood and the spruce stand soils in October, were examined. The results are summarized in tables 5 and 6.

216 specimens i.e. 51 % of the examined animals (maturus juniori, females and males) were identified to species. Specimens not possible to identify and/or damaged were classified as "Undetermined". This does not include other larvae than maturus junior. Larvae I and II were found both in the oak and the spruce samples. No praelarvae were found, which as mentioned before may be a consequence of the extraction technique.

All examined specimens except one belong to the genus *Eosentomon*. The remaining specimen, a larva II, belongs to the family Acerentomidae. It was found in the oak wood, sample G 6. Three species of *Eosentomon* were found: *E. delicatum* Gisin and *E. germanicum* Prell (Tuxen in letter 1978), and a third species which due to inappropriate mounting could not be identified with certainty. I think there is a fairly high probability that the species is *E. transitorium* Berlese. However, since this could not be verified, it will be called *E.* sp. in the rest of the paper.

The species composition of the identified *Eosentomon* spp. in the two habitats is presented in table 7. *E. germanicum* is dominating in both habitats. However, it seems like *E. delicatum* and *E.* sp. change frequency between the oak wood and the spruce stand soils. The species composition in total is significantly different between the two habitats ($p < 0.001$, $\chi^2 = 15.32$ d.f. = 2). Comparing the species in pairs the proportions are significantly dif-

Table 7. Species composition of identified *Eosentomon* spp. in the oak wood and the spruce stand samples

Species	Oak wood %	Spruce stand %
E. delicatum	18	4
E. germanicum	79	83
E. sp.	3	13
Sum of percentages	100	100
Number of specimens	67*)	149**)

*) 12 + 53 + 2 = 67; **) 6 + 124 + 19 = 149.

Table 8. Relationship between maturus juniori and imagines in the identified *Eosentomon* spp. Total of the oak wood and the spruce stand samples

	E. delicatum %	*E. germanicum* %	*E.* sp. %
Maturus juniori	11	26	38
Imagines	89	74	62
Sum of percentages	100	100	100
Number of specimens	18 (12 + 6)	177 (53 + 124)	21 (2 + 19)

ferent between *E. delicatum* and *E. germanicum* ($p < 0.01$, $\chi^2 = 8.33$ d.f. $= 1$), *E. delicatum* and *E.* sp. ($p < 0.001$, $\chi^2 = 11.38$ d.f. $= 1$) but not between *E. germanicum* and *E.* sp. ($p < 0.10$, $\chi^2 = 2.95$ d.f. $= 1$). The conclusion from these tests is that the relative frequencies between the species are different in the samples I have taken from the sample sites.

The proportions between maturus juniori and imagines in the identified species are summarized in table 8. Even if there is a slight difference ranging from 11 % maturus juniori in *E. delicatum* to 38 % in *E.* sp., there are no significant differences. As seen in tables 5 and 6 the proportions of maturus juniori in *E. germanicum* differ between the habitats. In the oak wood samples 19 % maturus juniori were found and in the spruce samples 29 %. This difference is not significant. In the other two species the number of collected animals is to small to evaluate differences between the proportions of maturus juniori and imagines in the habitats.

A considerable proportion of the collected Protura consists of larvae I and II. In the oak wood samples 35 % of the animals were larvae I and II, corresponding value for the spruce stand is 30 %. Unfortunately it has not been possible to identify these larvae to species. There is a difference between the proportions of larvae I and II in the two habitats. In the oak wood samples 31 % are larvae I and 69 % larvae II, in the spruce stand samples there are 84 % larvae I and 16 % larvae II. This is a significant difference between the proportions ($p < 0.001$, $\chi^2 = 32.36$ d.f. $= 1$).

The *E. germanicum* imagines could be examined for sex ratio. In total, for both habitats together, 55 % are females and 45 % are males. The oak samples have 70 % females and 30 % males, this difference is significant ($p < 0.01$, $\chi^2 = 6.72$ d.f. $= 1$). In the spruce samples a more even sex ratio was found: 48 % females and 52 % males.

4. Discussion

4.1. Protura distribution

Raw (1956) and Haarløv (1960) reached different conclusions regarding Protura dispersion. Raw found Protura to be highly aggregated, whereas Haarløv found them dispersed at random. It is important to notice that the population density of Protura is low

in the study by HAARLØV. As e.g. SKELLAM (1952) pointed out the distribution patterns at low densities are often approaching random. Conclusions regarding dispersion are therefore dependent on the obtained population density. The results from this study however support the conclusion of an aggregated distribution pattern among Protura.

Environmental factors have been proposed by several investigators to be responsible for aggregated distribution pattern among microarthropods in soil. POOLE (1961) suggested that environmental factors determine aggregation in Collembola, BERTHET & GÉRARD (1965) concluded the same about Oribatid populations. However, in a later study POOLE (1962) supposed that physical factors alone could not be responsible for the observed dispersion.

MACFADYEN (1963) stated that animals with patchy distribution must have some sort of habitat selection. A possible way for Protura in selecting habitat, is to react to environmental factors such as e.g. moisture. If an animal moves very slowly in moist air and more rapid in dry air, that is a simple way of habitat selection, since the chance to die of desiccation then is reduced. Several other factors, e.g. clumped food distribution i.e. hyphae and mycorrhiza, could of course also influence aggregation among Protura.

4.2. Protura population densities

It must be emphasized that far from the entire populations were extracted from the soil cores, e.g. praelarvae missing. Furthermore, only the 5 cm top layer of soil was included in the samples. It is uncertain how much of the Protura populations that inhabit the layers below 5 cm. TUXEN (1949) found *Eosentomon transitorium* homogeneously dispersed in the upper 3 cm of beech soil. At 4 and 5 cm depth they were more scarce. He supposed that Protura, in his study habitat, seldom occurred in layers below 5 cm, which also was the approximate depth of the humus. However, HAARLØV (1960) found *E. transitorium* in pasture soil as deep as 50—51 cm. It seems reasonable to suppose that Protura occupies at least the entire humus layer. Transferred to the sites of this study, which both had about 10 cm humus, perhaps the obtained estimates (see table 4) should be doubled to be more realistic.

A rough comparison can be made with other studies, which gave the following results for different habitats:

(1) Pasture: 1400/m^2(HEALY 1971 from SALT et al. 1948); 6680/m^2 (CURRY 1969); 7000/m^2 (HEALY 1971 from RAW 1956)-

(2) Beech wood: 6500/m^2 (HEALY 1971 from TUXEN 1949).

(3) Coniferous forests: (3.1.) spruce: 1500/m^2, 3900/m^2 (HUHTA & KOSKENNIEMI 1975), (3.2.) scots pine: 11,400/m^2, 16,000/m^2 (AXELSSON et al. 1973).

4.3. Protura population and species structure

When discussing the population and species structure (tables 5 and 6) one should bear in mind that only 51% of the specimens are identified to species. Furthermore, as many as 22% of the specimens in the spruce stand samples are classified as "Undetermined". Therefore one has to be careful about conclusions, especially about species structure. However, since *E. delicatum* differ in its general apperance from the two other species, it is likely that all specimens of *delicatum* are discovered and recognized.

The dominance of *E. germanicum* in both habitats is well in consistency with NOSEK (1975), who places *E. germanicum* as a "characteristic species" of the Nordic region. He also places *E. delicatum* and *E. transitorium* as "constant species". Both the "Northern taiga" and the deciduous forests in Sweden are referred to as "Nordic region". Whether *E. delicatum*, due to evolutionary reasons, has a preference for deciduous woodlands before coniferous forests is not known. The results from the present study might suggest that. However, according to NOSEK (1973) *E. delicatum* is found in many kinds of habitats both in Sweden and the rest of Northern Europe.

The most remarkable thing about the population age structure is the difference in proportions of larvae I and II between the habitats. Also the high percentage of larvae I and II in relation to the rest of the collected animals, is somewhat unexpected. TUXEN (1949) suspected that a breeding period for *E. transitorium* could be possible in May-June in Denmark. However, he found both larvae I and II in several months during the year. Again, because of the uncertainty of what species the larvae I and II belong to, one has to be careful about conclusions. The present results may point to differences in age structure between the populations in the two habitats.

The reason for the departure from sex-ratio 1:1 towards a female dominance in *E. germanicum* from the oak wood samples, is not known. TUXEN (1949) found *Acerella* females to be more common than males several times during his 17 months investigation period. He explained this by a higher mortality among the males.

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6. Summary · Zusammenfassung

To compare the Protura populations in oak and spruce woodland sites, soil samples were taken in October. The estimated population densities were 3500 Ind./m² (S.E. = 1100) in the oak wood soil and 8400 Ind./m² (S.E. = 4400) in the spruce soil. In November a second sampling was done in the spruce stand soil. This gave a density of 6500 Ind./m² (S.E. = 1200). The Protura distribution pattern turned out to be aggregated in both sites. From the 421 specimens in the October samplings 51% were identified to species. *Eosentomon delicatum*, *E. germanicum* and a third unidentified *Eosentomon* sp. were found. Although *E. germanicum* was dominating in both habitats, the species composition differed between the sites ($p < 0.001$). The larvaforms I and II (not identified to species) also differed in proportion between the habitats ($p < 0.001$). The females of *E. germanicum* were more than twice as numerous as the males in the oakwood samples ($p < 0.01$).

Die Distribution, Abundanz und Populationsstruktur von Proturen in zwei Waldhabitaten in Südwest-Schweden

Zu vergleichen war die Proturenpopulation im Eichen- und im Tannenwald. Die Erdproben wurden im Oktober entnommen. Die geschätzte Populationsdichte im Boden des Eichenwaldes betrug 3500 Ind./m² (S.E. = 1100) und die des Tannenwaldes 8400 Ind./m² (S. E. = 4400). Im November wurde zum zweiten Mal dem Tannenwald Erdproben entnommen. Dies ergab eine Dichte von 6500 Ind./m² (S. E. = 1200). Die Proturaverteilung zeigte eine Akkumulation in beiden Gebieten. Von den 421 Exemplaren, die von den Erdproben im Oktober stammten, konnten 51% als Arten identifiziert werden. *Eosentomon delicatum*, *E. germanicum* und eine dritte unbestimmte Art *E.* sp. wurden gefunden. Obwohl *E. germanicum* in beiden Habitats dominierte, zeigte sich, daß die Artenzusammensetzung in den beiden Gebieten unterschiedlich war ($p < 0.001$). Die Larvenstadien I und II (nicht bis zur Art identifiziert) unterschieden sich ebenfalls im Verhältnis zwischen den beiden Habitats ($p < 0.001$). Die Weibchen von *E. germanicum* waren doppelt so zahlreich wie die Männchen in den Proben aus dem Eichenwald ($p < 0.01$).

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